Environmental and Experimental Botany 162 (2019) 560–571

Contents lists available at ScienceDirect

Environmental and Experimental Botany

journal homepage: www.elsevier.com/locate/envexpbot

# Importance of whole plant dry matter dynamics for potato (*Solanum tuberosum* L.) tuber yield response to an episode of high temperature

Charles Otieno Obiero[a,b,*], Stephen Paul Milroy[a], Richard William Bell[b]

[a] Potato Research Western Australia, College of Science Health Engineering and Education, Murdoch University, 90 South Street Murdoch, Western, 6150, Australia
[b] Agriculture Discipline, College of Science Health Engineering and Education, Murdoch University, 90 South Street Murdoch, Western, 6150, Australia

ARTICLE INFO

*Keywords:*
Heat
Leaf area
Starch
Sucrose
Tuber initiation
Tuber growth

ABSTRACT

Potato is adapted to mild climates, but climate change may increase its exposure to more high temperature episodes of greater severity. However, there is limited information on the likely response of potato to high temperature episodes. We investigated the growth of potato exposed to an episode of high temperature before (Expt. 1) or after tuber initiation (Expt. 2). In both glasshouse experiments, plants were grown at 22 °C. At 35 days after planting (DAP) (Expt. 1) or 43 DAP (Expt. 2), plants were transferred to high temperature treatments of 26 or 30 °C for nine days then returned to 22 °C for 26 days. Tuber dry matter was reduced to a similar extent whether the high temperature episode occurred before or after tuber initiation. These effects were inconsistent with previously proposed mechanisms that attributed reduced tuber dry matter to starch synthase inhibition or increased gibberellic acid production. They were more consistent with insufficient whole plant carbon occasioned by reduced leaf area and continued shoot growth, particularly of the laterals, during and after the high temperature episode. Starch and sucrose distribution in the plants supported this but also suggested different mechanisms when the high temperature occurred before or after tuber initiation.

## 1. Introduction

Potato is increasingly exposed to episodes of high temperature due to climate change which can be expected to reduce its yields (Muthoni and Kabira, 2015; Hijmans, 2003; Pereira et al., 2008; Jovanovic et al., 2012; Haverkort, 1990). In some regions, such as Northwest China, potato crops already experience episodes that can last for more than seven days of temperatures above the 25 °C critical threshold for tuber growth (Hou et al., 2010). While some studies have examined long term exposure of potato to increased temperatures (Timlin et al., 2006; Lafta and Lorenzen, 1995; Menzel, 1985), limited understanding exists regarding the influence of episodes of high temperatures (typical of the field situation) on the physiology and growth of potato plants and tubers.

Episodes of high temperatures can occur at any stage of development during the growth of plants but thereafter plants often return to a lower temperature. Thus, the responses of plants during the high temperature period and after the end of the high temperature period become important. Prolonged soil and/or air temperatures above 25 °C impair tuber growth (Haverkort, 1990; Wheeler et al., 1986; Hawkes, 1978; Prange et al., 1990; Reynolds and Ewing, 1989) and can cause up to 100% loss in tuber dry matter (Lafta and Lorenzen, 1995; Menzel, 1980; Bushnell, 1927). However, most studies only consider the influence of the high temperatures at the tuber growth stage (Lafta and Lorenzen, 1995; Hancock et al., 2014). Further, in most studies the potato plants were exposed to long-term high temperatures sometimes lasting from planting until harvesting and the data collected at the end of that period (Timlin et al., 2006; Prange et al., 1990; Bushnell, 1927). Therefore, there are questions about the relevance of these studies to the actual temperature conditions experienced by field grown potato plants. Less is known about how potato plants behave under conditions of episodic high temperature. Does a return of plants to cooler conditions after the end of an episode of high temperatures allow the plant and tuber growth to recover or are there any persistent effects of the high temperature episode? Moreover, in the few studies in which the potato plants were exposed to some episode of high temperatures, no data were collected at the end of the high temperature period (Rykaczewska, 2015) so responses occurring during the high temperature event could not be separated from those occurring after the high temperature event.

In potatoes, the growth of other plants parts is reduced after tuber initiation (Moorby, 1978). However, potato plants exposed to

* Corresponding author. Current address: Jaramogi Oginga Odinga University of Science and Technology, School of Agricultural and Food Sciences, P.O. Box 210-40601, Bondo, Kenya.
*E-mail addresses:* otycha@gmail.com (C.O. Obiero), S.Milroy@murdoch.edu.au (S.P. Milroy), R.Bell@murdoch.edu.au (R.W. Bell).

https://doi.org/10.1016/j.envexpbot.2019.04.001
Received 22 January 2019; Received in revised form 23 March 2019; Accepted 2 April 2019
Available online 03 April 2019
0098-8472/ © 2019 Elsevier B.V. All rights reserved.

continuous high temperatures experience reduced dry matter partitioning to the tubers and increased shoot growth (Struik et al., 1989a; Borah et al., 1960; Struik et al., 1989b). Continuous high temperatures also alter the shoot structure in potatoes plants by promoting lateral shoot growth (Fleisher et al., 2006) which may contribute to the change in supply of photosynthates to the tubers (Ingram and McCloud, 1984; Boyd et al., 2002; Monteith and Moss, 1977). However, in studies of whole plant responses to continuous high temperatures, the responses in leaf expansion were inconsistent (Lafta and Lorenzen, 1995; Prange et al., 1990) but tuber yield was always reduced (Timlin et al., 2006; Lafta and Lorenzen, 1995). Thus, it is unclear whether impacts of high temperature episodes on whole plant carbon production and distribution could partly explain the reduction in tuber yields.

Depressed starch synthase activity is proposed as a mechanism that explains the reduction in tuber growth at continuous high temperatures. Starch synthase is responsible for starch deposition in storage organs including tubers (Edwards et al., 1999; Savin and Nicolas, 1996). At temperatures above 25 °C, starch synthase activity rapidly declines leading to less starch accumulation in the organ hence less growth (Keeling et al., 1993). Thus, potatoes grown at temperatures above 25 °C show reduced tuber growth (Mares and Marschner, 1980; Krauss and Marschner, 1984).

Increased production of gibberellins has also been proposed as a mechanism that influences tuber growth in potato plants exposed to high temperatures. Gibberellins are linked to three responses of the potato plant to temperature. Gibberellic acid (GA) inhibits tuber initiation and hence reduces the number of tubers produced per plant (Lovell and Booth, 1967; Menzel, 1983). It also stimulates both shoot growth and stem elongation leading to increased shoot dry matter and taller plants (Menzel, 1980; Lovell and Booth, 1967). Further, GA reduces the activity of starch synthase at the tuber level leading to repartitioning of the sucrose that would otherwise go to tubers into the shoots and stolons (Lovell and Booth, 1967; Mares et al., 1981; Booth and Lovell, 1972). However, the conclusions based on the inactivation of starch synthase and the increased production of GA at high temperatures were derived from studies in which potato plants were exposed to long-term effects of high temperatures without exposure to cooler conditions after the end of the high temperature period. Further, plants were never exposed to high temperatures before tuber initiation to investigate the subsequent impacts on tuber growth. Thus, important questions arise about what happens during and after an episode of high temperatures as is likely in the field situation. What mechanism (or mechanisms) controls the response of potato plants to an episode of high temperatures? Do the plants recover after an episode of high temperatures? Does an episode before tuber initiation have any impact on tuber growth and yield?

The diurnal cycle of temperature also has an influence on crop growth and yields. Literature suggests that high night-time temperatures could cause more harmful effect on tuber growth than the high daytime temperatures (Driver and Hawkes, 1943; Gregory, 1956). The same impact is also shown in other plant species such as rice and wheat (Prasad et al., 2008; Morita et al., 2005). In this study, however, the daytime and nighttime temperatures were maintained constant. The study investigated the growth responses of potato plants during and after the end of a 9-day episode of high temperature applied either shortly before or after tuber initiation.

## 2. Materials and methods

Two experiments (Expt. 1 and 2) were conducted in glasshouses at Murdoch University, Perth (32° 04′ S; 115° 50′ E) Western Australia. Expt. 1 involved application of an episode of high temperature shortly before tuber initiation while in Expt. 2, the same high temperatures were applied after tuber initiation was confirmed. Expt. 1 was conducted from December 2015 to March 2016 and Expt. 2 from March to June 2016.

### 2.1. Experimental design and treatment structure

Each experiment had three treatments: the control, in which plants were grown and maintained at a constant temperature of 22 °C until final sampling, and two high temperature treatments in which plants were exposed to either 26 °C or 30 °C for nine days. In Expt. 1, the high temperature episode (before tuber initiation) commenced 35 days after planting (DAP). In Expt. 2, the high temperatures episode (after tuber initiation), commenced 43 DAP. After nine days at the higher temperatures, all plants were returned to 22 °C and grown for a further 25 days until final sampling, being 70 DAP (Expt. 1) and 77 DAP (Expt. 2).

### 2.2. Plant management

The glasshouses were heated and cooled by reverse cycle air conditioners. Photoperiod ranged from 14 h in December to 12 h in March (Expt. 1) and from 12 h in March to 10 h in June (Expt. 2). In both experiments, the average relative humidity during the high temperature period was 48% in 30 °C treatment, 84% in the 26 °C treatment and 68% in the 22 °C treatment. The average air temperature in the nominally 30 °C treatment was 31 °C. The mean temperature of the growth media measured 10-cm below the surface using iButton Temperature Loggers DS1904 L (ALPHAOMEGA Electronics, Spain) was 30, 25 and 23 °C, respectively, in the 30, 26 and 22 °C treatments.

Photoperiod can affect tuber development in potato (Van Dam et al., 1996). While there was a difference in the photoperiod between the two experiments, there was little difference in the observed tuber dry matter per plant for the control treatments in the two experiments. In Expt. 1, there was 60 g tuber dry matter per plant at 70 DAP and in Expt. 2, there was 70 g per plant at 77 DAP (see Fig. 1). It should also be noted that potato is grown and harvested all year round in Western Australia.

In both experiments, uniformly sprouted seed potatoes (cv. Royal Blue) were planted at a depth of 10 cm in 24-L woven potting bags filled with growth medium. The bags were already in the glasshouse at 22 °C. The growth medium was prepared by thoroughly mixing 40 g of Osmocote, 40 g of Grower's Blue, 20 g dolomite ($CaMgCO_3$), 12 g lime ($CaCO_3$) with 29.5 kg of a commercial potting mix comprising 2 parts composted pine bark, 2 parts coarse river sand, and 1-part coco peat (Richgro, Western Australia). Additional Osmocote was applied on 35 DAP (Expt. 1) or 43 DAP (Expt. 2) at the rate of 16 g per plant. Osmocote contained 14% N, 3% P, 18% K and 3% Mg. Grower's Blue contained 12% N, 5% P, 14% K, 9.8% S. The growth medium was kept moist throughout the experiment.

One vigorously growing shoot per plant was selected and the rest were removed 14 DAP in both experiments. Thereafter, extra shoots were removed as soon as they emerged. The main shoot was supported by a fibreglass stake. Extra plants were maintained for checking to ensure that the high temperatures were applied at the correct stage relative to tuber initiation.

### 2.3. Data collection

Three destructive samplings were conducted in each experiment. The first sampling was conducted on the day before commencement of the high temperature treatment, the second at the end of the high temperature episode and the third at the end of the experiment after plants had been grown back at 22 °C for 26 days.

At each sampling, four (Expt. 1) and six (Expt. 2) plants were sampled for leaf area, plant height, dry weights (shoot[1], main shoot[2], lateral shoots[3], main stem[4], leaves on the main shoot, leaves on lateral

[1] Shoot – All the above ground plant part of the potato plant including the main stem, the branches (lateral shoots), petioles and leaves.
[2] Main shoot – The shoot without the branches (lateral shoots).
[3] Lateral shoots – Branches of the main shoot.
[4] Main stem – The main shoot without branches, leaves and petioles.

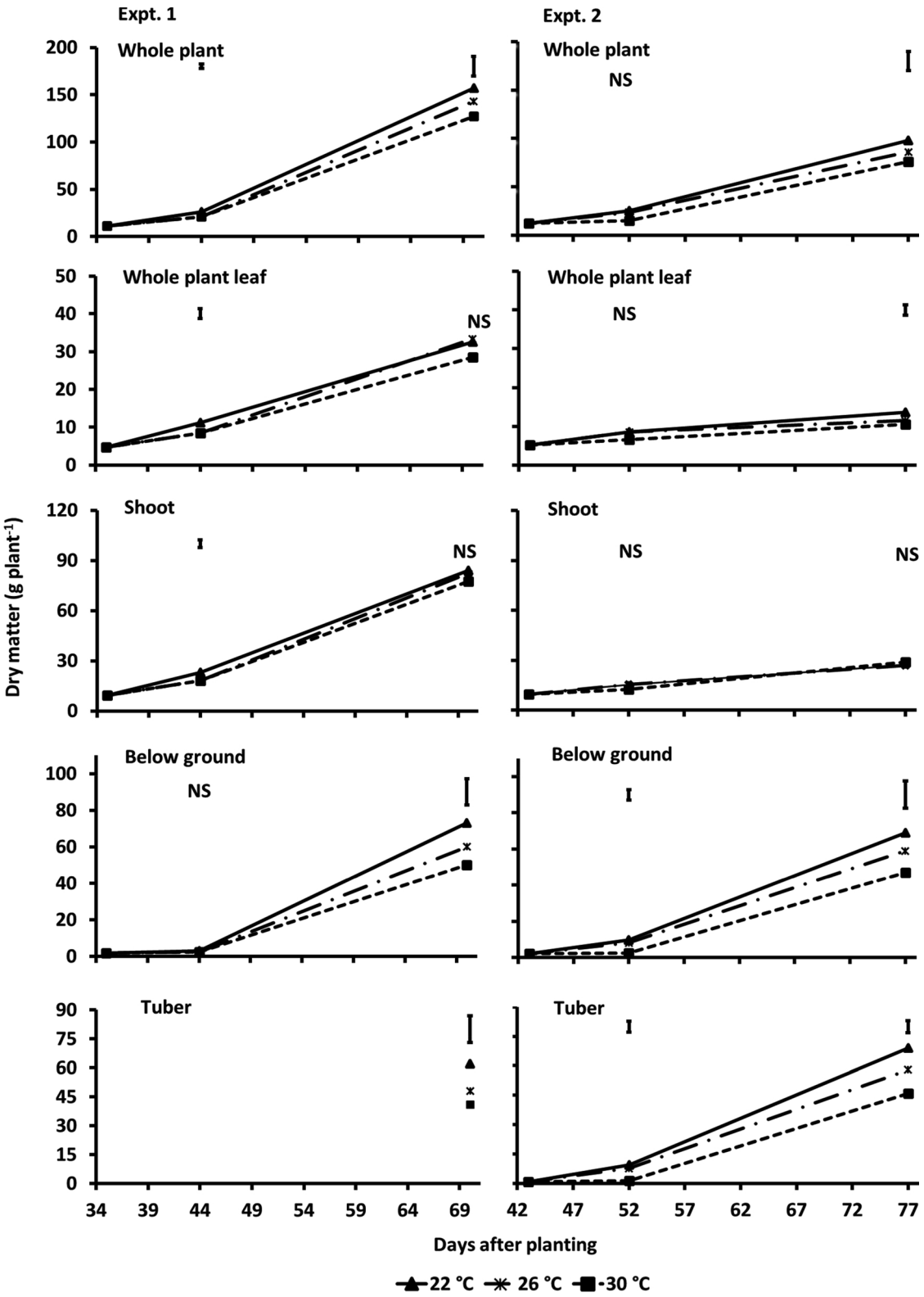


**Fig. 1.** Whole plant, leaf, shoot, below ground and tuber dry matter per plant as influenced by a 9-day episode of high temperatures applied before (Expt. 1) or after (Expt. 2) tuber initiation. The high temperatures were applied from 35 to 44 (Expt. 1) and 43 to 52 (Expt. 2) days after planting (DAP), respectively. Error bars are LSD at P = 5%. NS = Not significant.

shoots, senesced leaves on the main shoot, senesced leaves on lateral shoots, and tubers), the total number of tubers and the tuber number in two size categories (tubers with diameter greater than or less than 2.5 cm). All laminae were removed from the petioles. The senesced sections of laminae were also removed after which the green leaf area was measured using a portable laser leaf area meter (C1-202, CID Bio-Sciences Inc. USA). All plant parts were put in paper bags and dried in a forced draught oven at 60 °C to constant weight.

### 2.4. Analysis of water-soluble carbohydrates and starch

Analysis of starch and water-soluble carbohydrates of potato plants were conducted at the Centre for Biosecurity and Food Security, Murdoch University. The water-soluble carbohydrates were estimated through ultra-high-performance liquid chromatography (UHPLC) and starch estimated colorimetrically using the phenol-sulphuric method and a UV–vis spectrophotometer.

#### 2.4.1. Plant samples

Dried samples of the tubers, main stems and the leaves from the main shoots were ground into fine powder using an electric blender (Rocket Blender XJ-11401BO, Bella, USA). The ground samples were kept in 50-ml air tight jars in the dark until analysed. Water-soluble carbohydrates and starch were analysed in the tubers from all treatments but in the main stems and the main shoot leaves only analysed for the control and the 30 °C treatment. A total of 112 samples: 28 (Expt. 1) and 84 (Expt. 2) were analysed for the water-soluble carbohydrates. Each sample consisted of either four (Expt. 1) or 6 (Expt. 2) biological replicates.

#### 2.4.2. Estimation of the water-soluble carbohydrates

1 mg ml$^{-1}$ stock solutions for fructose (99%), glucose (99.5% Gas Chromatography (GC)) and maltose monohydrate were prepared by dissolving 25 mg of the sugar in 25 ml of 50% aqueous methanol (99.9% HPLC grade). A stock solution of 10 mg sucrose ml$^{-1}$ (99.5% GC) was also prepared by dissolving 500 mg of the dry sugar in 50 ml of 50% aqueous methanol. The standards were kept sealed in the dark at 4 °C.

On the day prior to the analysis of the samples, a dilution series of the standards were made in 50% aqueous methanol. The concentrations were 0.1, 0.3, 0.5, 0.7 and 1.0 mg ml$^{-1}$ for each of fructose, glucose, maltose and sucrose. Two additional concentrations, 1.5 and 2.0 mg ml$^{-1}$, were included for the sucrose standard. The dilutions were also kept sealed in the dark at 4 °C.

The water-soluble carbohydrates were extracted from the plant samples using a method adapted from Duarte-Delgado et al. (2015). Eight millilitres of 50% aqueous methanol were added to 500 mg of the dry, powdered plant material. A blank sample of 8 ml of the 50% aqueous methanol was also prepared. The samples were cleaned for 5 min at 25 °C in a digital ultrasonic cleaner (Model No. PS-20A, Branson Ultrasonics USA). The samples were then extracted for 60 min at 17 rpm in an 80 °C water bath. The extracts were cooled to 22 °C for 30 min then transferred into 2-ml vials and centrifuged for 30 min at 6000 rpm. The clear extracts were filtered through 0.22 µm filters into 2-ml HPLC vials. The filtered extracts were kept in the dark at 4 °C until analysed. The samples extracted for the water-soluble carbohydrates had no analytical replicates; the extraction was conducted only on the biological replicates. Mass Lynx v4.1 software was used for data acquisition and peak integration. Before the samples were injected into the UHPLC system, a blank sample containing only double-distilled (DD) water followed by two runs from the 1 mg ml$^{-1}$ quality control (QC) sucrose standard were used to condition the column. The samples and sugar standards were then injected at random. The 1 mg ml$^{-1}$ QC sucrose standard was also injected after every 10 samples for a system stability check.

A Waters™ Acquity UHPLC system equipped with a 20 µl loop and a High-Resolution Mass Detector (Waters™ Q-Tof Premier Micromass Technology) was used to simultaneously separate and analyse the sugars. The system was run at 0.13 ml min$^{-1}$ using a Shodex $NH_2$P-40 2B, 4 µM, 2.0 × 50 mm analytical column protected by a Shodex Asahipa $NH_2$P-50G 2A, 5 µm, 2.0 × 10 mm guard column. The column was at 35 °C and 250 psi. The sample temperature was 4 °C. An isocratic mobile phase of 75% aqueous acetonitrile (99.9% HPLC grade) and 0.05% $NH_3$ (35%) was used. The injection volume was 2.0 µl.

The sample run time was 15 min. This allowed 10 min for cleaning the column and 5 min for injecting the sample. The cleaning procedure involved injecting an isocratic solution of 90% aqueous acetonitrile for 5 min followed by a 75% aqueous acetonitrile solution for 5 min. The sugar sample was injected during the last 5 min.

#### 2.4.3. Estimation of starch content

Stock solution containing 1 mg ml$^{-1}$ glucose standard was prepared by dissolving 50 mg of glucose in 50 ml of 0.7 M HCl (37% ACS[5] reagent). A glucose dilution series was prepared using 0.7 M HCl to give: 0.02, 0.04, 0.06, 0.08 and 0.1 mg ml$^{-1}$. The dilutions were made in duplicate one day before the plant samples were analysed and kept sealed in the dark at 4 °C.

Starch from the plant samples was hydrolysed using a method adapted from Haebel et al. (2008). About 50 mg (tuber) or 200 mg (stem or leaf) sample was mixed with 20 ml of 0.7 M HCl. A blank sample of 20 ml 0.7 M HCl and two standard samples containing 20 and 50 mg of the starch standard were also prepared. The mixture was then cleaned in the ultrasonic cleaner for 5 min and then hydrolysed for 3 h in a 99 ± 1 °C water bath. The hydrolysate was cooled at room temperature for 30 min. Two ml of the cooled hydrolysate were transferred into a 2-ml centrifuge vial and kept sealed in the dark at 4 °C until analysed. Two samples of 20 and 50 mg starch standard and one QC tuber sample were included in each batch of samples processed.

The glucose content of the hydrolysate was estimated using a UV-vis Spectrophotometer (Beckman Instruments, Australia Pty Ltd). The method was adapted from Dubois et al. (1956) and Albalasmeh et al. (2013). Two millilitres of the hydrolysate were centrifuged for 15 min at 6000 rpm. One ml of the supernatant was diluted 50 times by adding 49 ml of DD water. One ml of the diluted hydrolysate was pipetted into 15-ml Pyrex test tube. One ml of the glucose standard concentrations was also pipetted into separate 15-ml Pyrex test tubes. One ml of 5% fleshly prepared phenol was added, followed by 5 ml of concentrated sulphuric acid. The test tubes were then vortexed at 2000 rpm for 30 s and cooled at room temperature for 30 min. To the cooled samples, 6 ml of DD water was added and the samples vortexed for 30 s. The test tubes were left to equilibrate at room temperature for 15 min. The absorbance of each sample was read at 490 nm.

Only sucrose was detected in the analysis of the water-soluble carbohydrates. Starch and sucrose content (g plant$^{-1}$) were calculated based on the measured concentration and the dry matter of the plant part.

### 2.5. Data analysis

All variables were subjected to one-way analysis of variance (ANOVA) through the General Linear Model (GLM) procedure of the Statistical Analysis Software (SAS), University Edition (SAS Institute, North Carolina, USA). Number and size distribution of tubers per plant were square root transformed to achieve homogeneity of variance but only the back-transformed data are reported. Analysis of leaf senescence was performed on the percent of the senesced leaf dry matter in relation to the whole plant leaf dry matter per plant. The significant means were compared using the Fisher's Least Significant Difference (LSD) and reported at 5% level of probability unless otherwise specified.

## 3. Results

### 3.1. Whole plant dry matter and partitioning

In Expt. 1, the tubers had not formed by the end of the high temperature period (44 DAP) (Fig. 1). In Expt. 2, there was 85% less tuber dry matter in the 30 °C treatment than the control at the end of the high

[5] ACS – American Chemical Society.

temperature period. At the final sampling, there was 34% (Expt. 1) and 33% (Expt. 2) less tuber dry matter per plant in the 30 °C treatment than the control. In the 26 °C treatment of Expt. 2, there was also 16% less tuber dry matter per plant than in the control.

Whole plant dry matter was 19% less in the 30 °C treatment than the control in Expt. 1, both at the end of high temperature period and at the final sampling (Fig. 1). In Expt. 2, treatments were not different at the end of the high temperature period but at the final sampling there was 22% less whole plant dry matter in the 30 °C treatment than the control. Whole plant leaf dry matter was 24% less than the control in the high temperature treatments at the end of the high temperature period of Expt. 1, but at the final sampling, there were no differences among the treatments. In Expt. 2, treatments were not different at the end of the high temperature period. At the final sampling, there was 22% less whole plant leaf dry matter in the 30 °C treatment than the control.

The below ground dry matter at the end of the high temperature period of Expt. 1 was the same in all treatments; tubers had not been formed in any treatments. However, at the final sampling, plants in the 30 °C treatment had 32% less below ground dry matter than the control. In Expt. 2, the below ground dry matter per plant in the 30 °C treatment was 75% less than the control at the end of the high temperature episode while at the final sampling, the difference was only 32%.

Dry matter partitioning between the tuber and the whole plant was altered differently by the 9-day episode of high temperatures in the two experiments. In Expt. 1, there was no change in biomass partitioning between the tubers and the whole plant either at the end of the high temperature or at the final sampling. In Expt. 2, dry matter partitioning to the tubers decreased by 76% (at the end of the high temperature period) and 16% (at the final sampling) in the 30 °C treatment than in the control. Importantly, the shoot continued to accumulate dry matter during and after the end of the high temperature period in both experiments.

### 3.2. Shoot biomass partitioning and elongation

There was 20–22% less main shoot dry matter per plant (i.e. the shoot without the laterals) in the high temperature treatments than the control at the end of high temperature period in Expt. 1 (Fig. 2) but, there was no significant among the treatments at the final sampling. In Expt. 2, plants in all treatments had the same dry matter on the main shoot both at the end of the high temperature period and at the final sampling. At the end of the high temperature period, plants in all treatments had partitioned the same proportion of dry matter to the lateral shoots relative to the main shoot. This also held for the final sampling in Expt. 1, although there was some tendency for more dry matter partitioning to the lateral shoots than the main shoot in the 30 °C treatment. By the final sampling of Expt. 2, a higher proportion of shoot dry matter had been partitioned to the lateral shoots in the 30 °C treatment than in the control.

In Expt. 2, plants in the 30 °C treatment were 22% shorter than the control at the end of the high temperature period (Fig. 3) but by the final sampling of both experiments, plants in all treatments were of the same height in both experiments.

### 3.3. Number and size distribution of tubers per plant

In both experiments, plants in all treatments had the same total number of tubers and number of tubers with diameter of more than 2.5 cm (Table 1). However, there were 45% more tubers with the diameter of less than 2.5 cm in the 30 °C treatment than in the control at the final sampling of Expt. 2.

### 3.4. Leaf expansion and senescence

At the end of the high temperature period in both experiments, there was approximately 35% less leaf area per plant in the 30 °C treatment than in the control (Fig. 4). By the final sampling, all treatments in Expt. 1 had the same total leaf area. In Expt. 2 however, there was no recovery of leaf area. Plants in the 30 °C treatment at final harvest had approximately 23% less whole plant leaf area than the control.

The leaf area on the main shoot in the 30 °C treatment was approximately 35% less than the control at the end of the high temperature period in both experiments. At the final sampling, the main shoot leaf area in the 30 °C treatment was 41% (Expt. 1) and 37% (Expt. 2) less than in the control. In Expt. 2, the main shoot leaf area in the 26 °C treatment was also 25% less than the control at the final sampling. Not all treatments had developed lateral branches at the end of the high temperature period so there was insufficient data for analysis at that stage in either experiment. At the final sampling, leaf area of the lateral shoots relative to main shoot was 60% (Expt. 1) and 56% (Expt. 2) higher in the 30 °C treatment than in the control.

The high temperature period markedly increased leaf senescence in Expt. 2, particularly on the main shoot (Table 2). At the final sampling the main shoot had 58% (26 °C treatment) and 137% (30 °C treatment) more senescence than the control. Leaf senescence on the lateral shoots was not significantly different among the treatments.

### 3.5. Tuber sucrose concentration and content

At the final sampling of Expt. 1, plants in the 26 °C treatment had 12% lower sucrose concentration and 63% lower sucrose content than in the control (Fig. 5). In Expt. 2, at the end of the high temperature period there was 28% (26 °C) and 45% (30 °C) lower sucrose concentration and 92% (30 °C) lower sucrose content in the tubers of the high temperature treatments than the control. At the final sampling, there was no significant difference in sucrose concentration among treatments. The tubers in the 30 °C treatments were 31% lower in sucrose content than the control. Between the two samplings, sucrose content of the tubers in the 30 °C treatment had increased 16-fold whereas that of the tubers in the control and the 26 °C treatments, had only increased 2 to 3-fold during the same period. Comparing the two experiments, at the final sampling of Expt. 1, sucrose concentration and content were reduced in the tubers of the 26 °C treatment compared to the control. In Expt. 2, sucrose concentration was not significantly affected by any treatment and only the content in the 30 °C treatment was lower than the control.

### 3.6. Tuber starch concentration and content

At the final sampling of Expt. 1, tubers from all treatments had the same starch concentration but the starch content of the tubers in the high temperature treatments were 26% (26 °C) and 33% (30 °C) lower than in the control (Fig. 6).

At the end of the high temperature period of Expt. 2, there was 7% (26 °C) and 21% (30 °C) lower starch concentration and 87% (30 °C) lower starch content in tubers in the high temperature treatments than in the control. At the final sampling, starch concentration and content of the tubers were still lower in the high temperature treatments. In the high temperature treatments there was 16% (26 °C) and 5% (30 °C) lower starch concentration and 29% (26 °C) and 36% (30 °C) lower starch content in the tubers than in the control. Notably, the starch concentration in the 30 °C treatment increased by 26 g 100 $g^{-1}$ of tuber dry matter between the end of the high temperature period and the final sampling. In the control and the 26 °C treatment, the increase was only by 10.6 (control) and 12.4 g (26 °C treatment) 100 $g^{-1}$ of tuber dry matter. Comparing the results at the final sampling of the two experiments, starch concentration was only reduced relative to the control, in the tubers of the high temperature treatments in Expt. 2. However, starch content was lower in the high temperature treatments in both experiments and the reductions were of a similar extent.

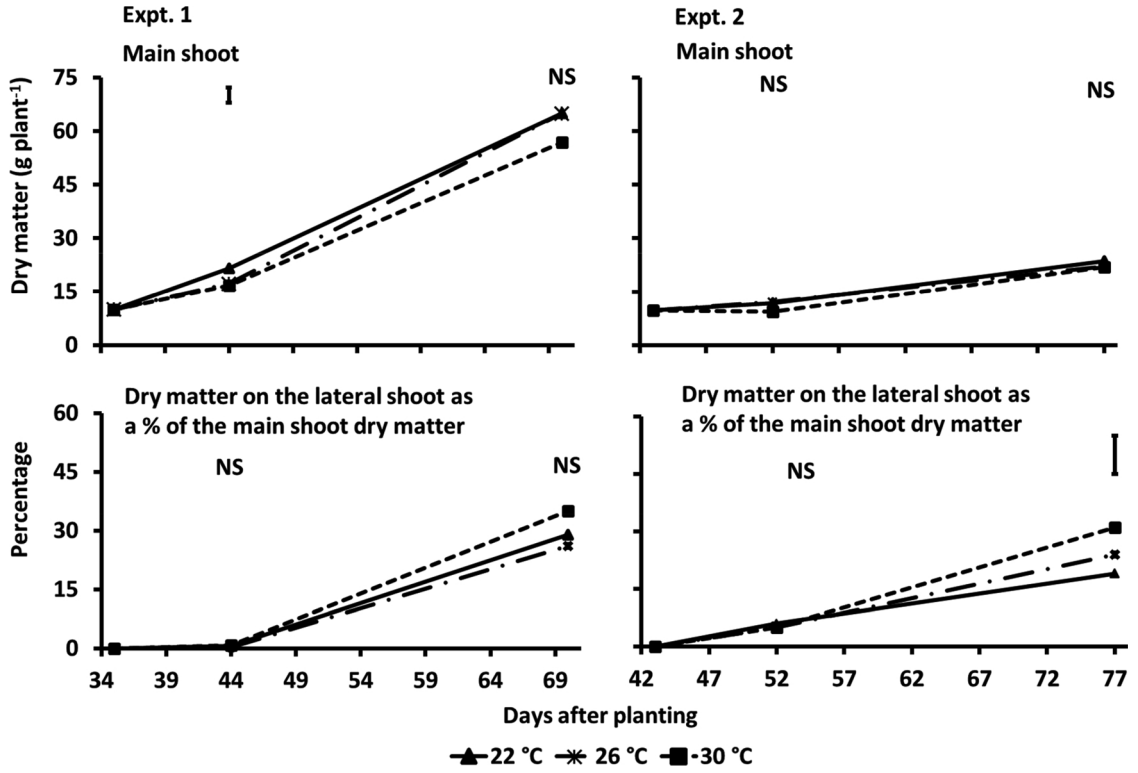


**Fig. 2.** The main shoot dry matter per plant and the dry matter on the lateral shoot as a percentage of the main shoot dry matter as influenced by an episode of high temperatures applied before (Expt. 1) or after (Expt. 2) tuber initiation. The high temperatures were applied from 35 to 44 (Expt. 1) and 43 to 52 (Expt. 2) DAP, respectively. Error bars are LSD at P = 5%. NS = Not Significant.

### *3.7. Sucrose concentration and content of the main shoot leaves and stems*

In Expt. 1, the main shoot leaves of the 30 °C treatment were 65% higher in sucrose concentration and 47% higher in sucrose content relative to the control at the final sampling. However, neither the concentration nor the content of sucrose in the main stems differed between treatments (Fig. 7). In Expt. 2, treatments were not different in either sucrose concentration or content of the main shoot leaves or the main stems at the end of the high temperature period. At the final sampling, sucrose concentration in the main shoot leaves was still not significantly different among treatments. However, the sucrose content in the main shoot leaves was 55% lower in the 30 °C treatment than in the control. The main stem in 30 °C treatment was 57% lower in concentration and 55% lower in sucrose content than the control. Overall, compared to the control, more sucrose accumulated in the main shoot leaves of the high temperature treatments in Expt. 1. The main stems were not significantly different among treatments. In Expt. 2, there was less sucrose content in the main shoot leaves of the high temperature treatments. Further, the main stems had both lower sucrose concentration and content in this experiment.

### *3.8. Starch concentration and content of the main shoot leaves and stems*

At the final sampling of Expt. 1, there was 13.4% higher starch concentration but 29.4% lower starch content in the main shoot leaves in the 30 °C treatment than the control (Fig. 8). Starch concentration in the main stems was not significantly different among treatments but the

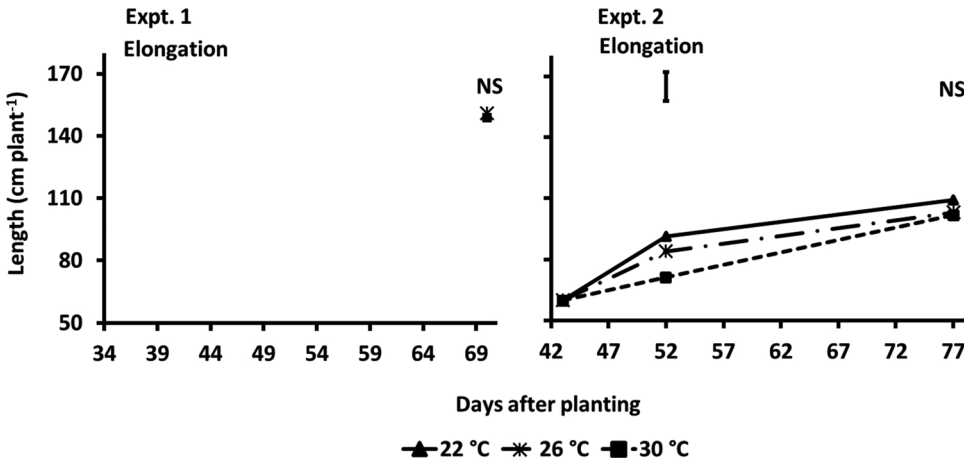


**Fig. 3.** The length of the main stem per plant as influenced by an episode of high temperatures applied before (Expt. 1) or after (Expt. 2) tuber initiation. The high temperatures were applied from 35 to 44 (Expt. 1) and 43 to 52 (Expt. 2) DAP, respectively. Error bars are LSD at P = 5%. NS = Not Significant.

**Table 1**
Total number and size distribution of tubers per plant as affected by a 9-day episode of high temperatures applied before (Expt. 1) or after (Expt. 2) tuber initiation. The high temperatures were applied from 35 to 44 (Expt. 1) and 43 to 52 (Expt. 2) days after planting (DAP), respectively. Analysis was conducted on square root-transformed data. Only back-transformed means are presented in the table. D = tuber diameter at the widest part.

| DAP | | 22 °C | 26 °C | 30 °C | LSD $_{0.05}$ |
|---|---|---|---|---|---|
| Expt. 1 (Before tuber initiation) | | | | | |
| 70 DAP | **Total** | **28** | **35** | **28** | **NS** |
| | D > 2.5 cm | 11 | 11 | 9 | NS |
| | D < 2.5 cm | 17 | 24 | 19 | NS |
| Expt. 2 (After tuber initiation) | | | | | |
| 52 DAP | **Total** | **18.6** | **16.5** | **18.1** | **NS** |
| | D > 2.5 cm | 1.3 | 1.5 | 0.0 | NS |
| | D < 2.5 cm | 17.3 | 15.0 | 18.1 | NS |
| 77 DAP | **Total** | **21.2** | **20.6** | **30.7** | **NS** |
| | D > 2.5 cm | 8.7 | 6.7 | 8.0 | NS |
| | D < 2.5 cm | 12.5b | 14.0ab | 22.7a | 9.2 |

Means marked with the same letter within a row are not significantly different, NS = Not significant.

**Table 2**
Whole plant, main shoot and lateral shoots senesced leaf dry matter per plant as affected by a 9-day episode of high temperatures applied after (Expt. 2) tuber initiation. Percent leaf senescence is based on respective component of leaf dry matter.

| Growth parameter | Senesced leaves as % of the whole plant leaf dry matter in Expt. 2 | | | | |
|---|---|---|---|---|---|
| | DAP | 22 °C | 26 °C | 30 °C | LSD $_{0.05}$ |
| Whole plant leaves | 52 DAP | 2.1b | 2.1b | 7.2a** | 2.56 |
| | 77 DAP | 15.9c** | 24.4b* | 34.2a | 8.44 |
| Main shoot leaves | 77 DAP | 16.9c*** | 26.7b* | 40.0a | 9.19 |
| Lateral shoot leaves | 77 DAP | 11.2 | 14.8 | 14.0 | NS |

*, **, and *** means significant at $p < 0.05$, 0.001 and, 0.0001 respectively, means with same letters in the same row are not significantly different, NS = Not significant.

main stems of plants in the 30 °C treatment had 12.4% lower starch content than the control. In Expt. 2, treatments were not different in either starch concentration or content of the main shoot leaves or the

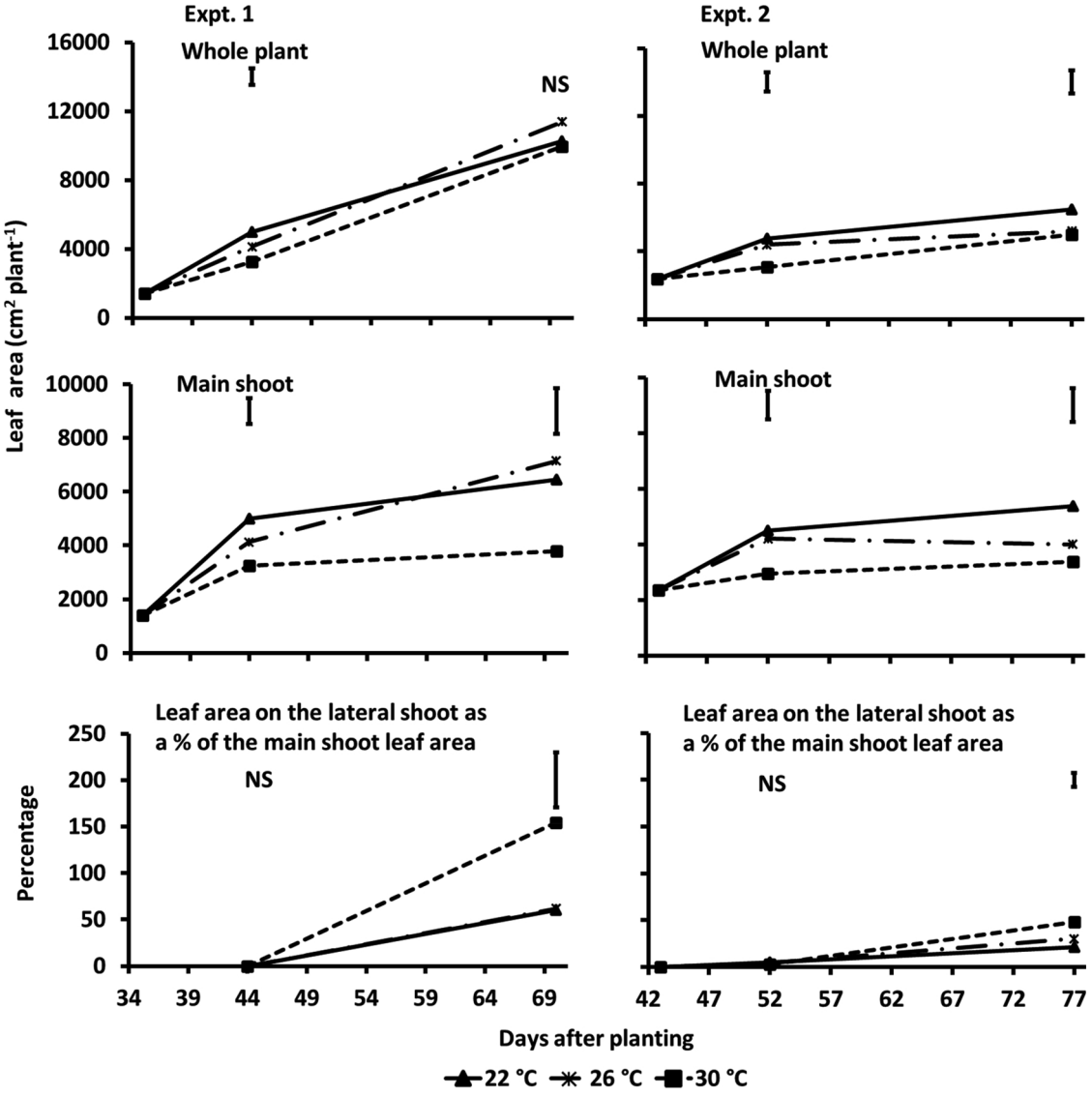


**Fig. 4.** Whole plant, main shoot and lateral shoot leaf area per plant as influenced by a 9-day episode of high temperatures applied before (Expt. 1) or after (Expt. 2) tuber initiation. The high temperatures were applied from 35 to 44 (Expt. 1) and 43 to 52 (Expt. 2) days after planting (DAP), respectively. Error bars are LSD at P = 5%. NS = Not Significant.

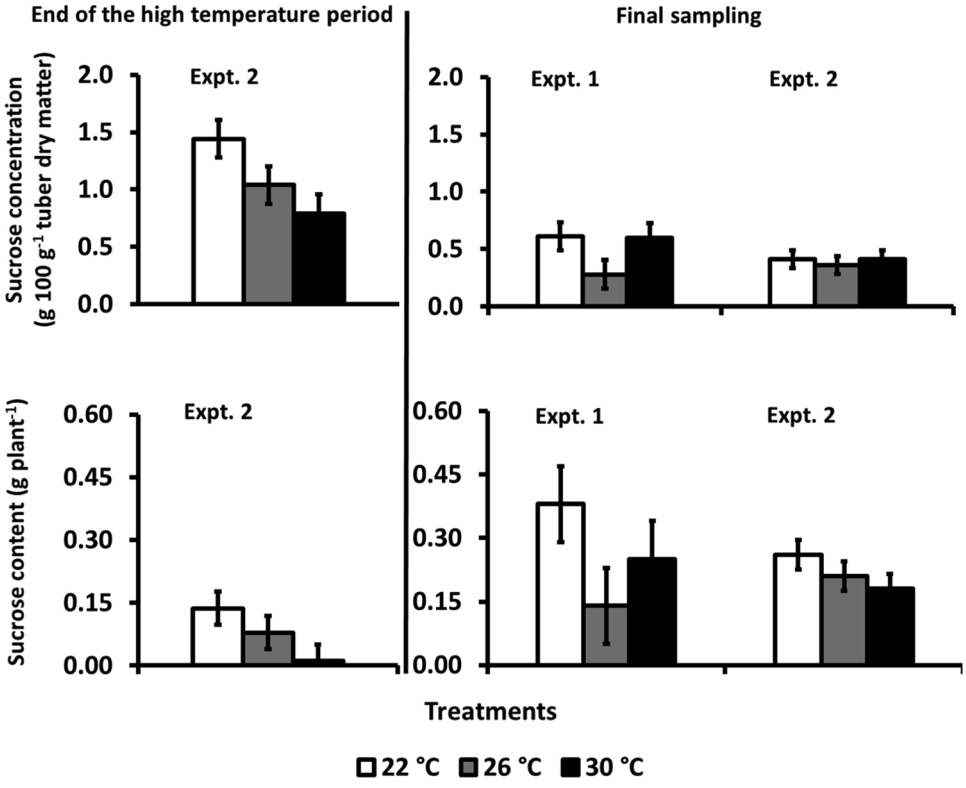


**Fig. 5.** Sucrose concentration and content in the tubers at the end of the high temperature period (Expt. 2) and at the final sampling (Expt. 1 and 2) as influenced by a 9-day episode of high temperatures applied before (Expt. 1) or after (Expt. 2) tuber initiation. The high temperatures were applied from 35 to 44 (Expt. 1) and 43 to 52 (Expt. 2) days after planting (DAP), respectively. Error bars are LSD at P = 5%.

main stems at the end of the high temperature period. At the final sampling, the 30 °C treatment had 5% higher starch concentration and 38% less starch content in the main shoot leaves than in the control. In the main stems, there was 5% lower starch concentration in the 30 °C treatment than in the control. However, starch content in the main stems was not different among treatments.

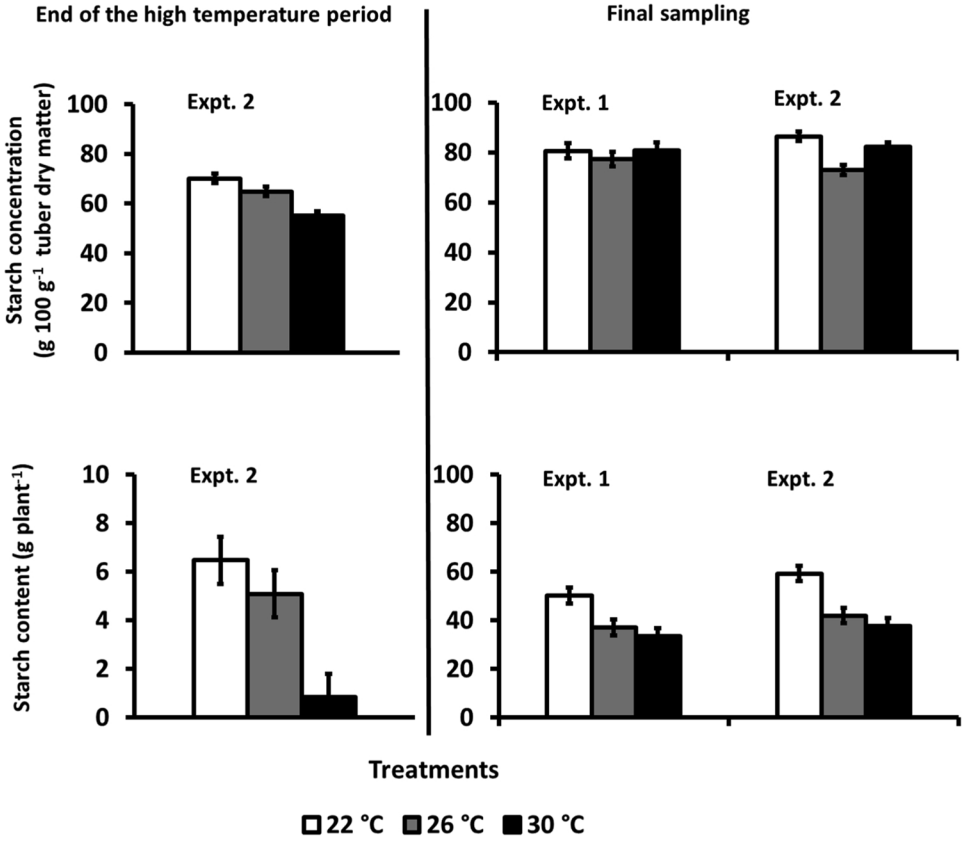


**Fig. 6.** Starch concentration and content in the tubers at the end of the high temperature period (Expt. 2) and at the final sampling (Expt. 1 and 2) as influenced by a 9-day episode of high temperatures applied before (Expt. 1) or after (Expt. 2) tuber initiation. The high temperatures were applied from 35 to 44 (Expt. 1) and 43 to 52 (Expt. 2) days after planting (DAP), respectively. Error bars are LSD at P = 5%.

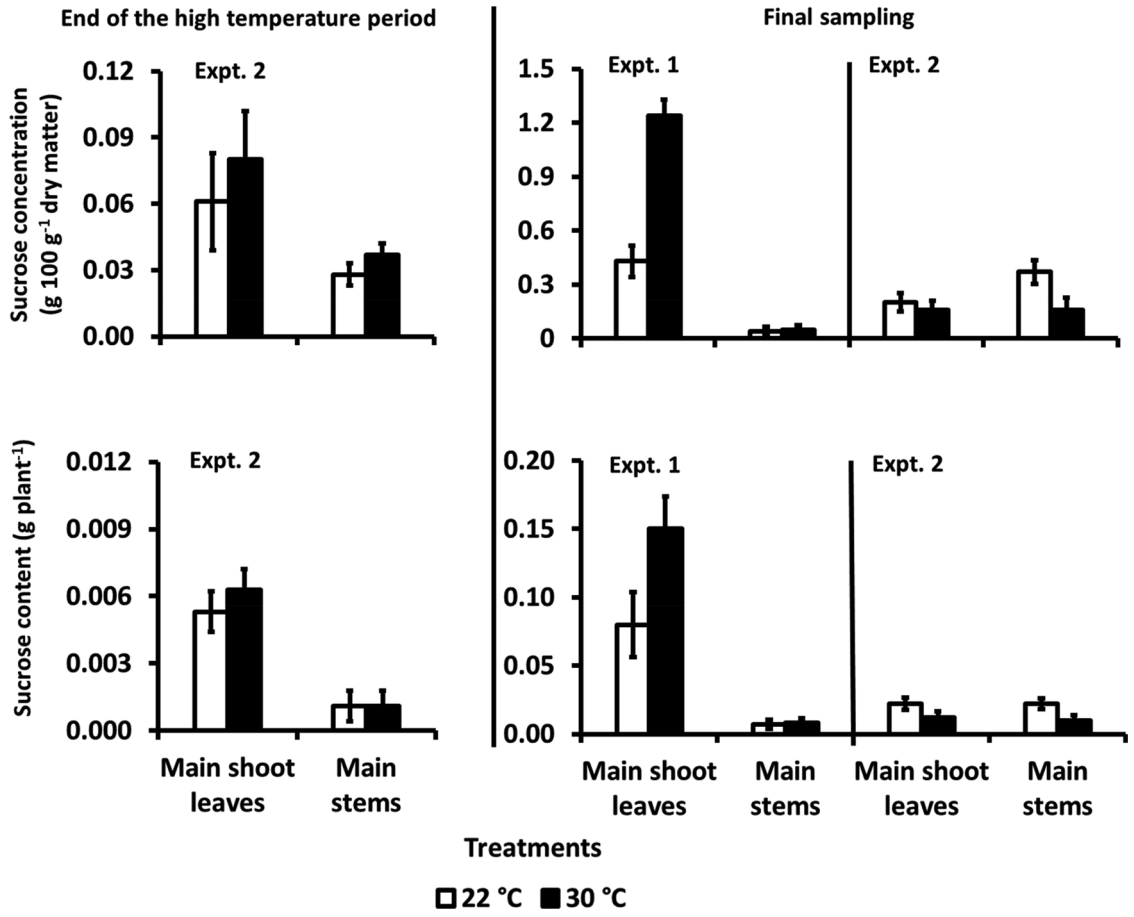


**Fig. 7.** Sucrose concentration and content in the main shoot leaves and stems at the end of the high temperature period (Expt. 2) and at the final sampling (Expt. 1 and 2) as influenced by a 9-day episode of high temperatures applied before (Expt. 1) or after (Expt. 2) tuber initiation. The high temperatures were applied from 35 to 44 (Expt. 1) and 43 to 52 (Expt. 2) days after planting (DAP), respectively. Error bars are LSD at P = 5%.

## 4. Discussion

The reduced tuber dry matter at the end of the high temperature period relative to the control plants is consistent with previous studies (Lafta and Lorenzen, 1995; Kooman, 1995; Marinus and Bodlaender, 1975; Kim et al., 2017). However, there are two important novel findings from the present study. Firstly, the reduction in tuber dry matter in Expt. 1 was very similar to that in Expt. 2 even though there were no tubers present when the high temperature episode was applied. Secondly, in Expt. 2, tuber dry matter accumulation in the high temperature treatments (26 and 30 °C) continued to be suppressed relative to the control (22 °C) after the end of the high temperature episode, even though the plants were growing at 22 °C. In both cases, the suppression of tuber growth due to the high temperature treatments occurred under temperatures that should have been favourable for tuber growth.

The reduction in tuber growth due to the high temperature episode can be largely attributed to the reduction in the leaf area in conjunction with the continued shoot growth. In both experiments, the high temperature treatments only had about 60% of the leaf area on the main shoot relative to the control both at the end of the high temperature period and at the final sampling. This reduction in the main shoot leaf area both at the end of the high temperature period and at the final sampling means that the whole plant carbon production was negatively influenced even if the high temperatures did not significantly impair the photosynthetic efficiency of the leaves, as has been indicated in some studies (Wolf et al., 1990). While total shoot biomass was not altered by the high temperatures, there was a change in the architecture of the shoots, resulting from the expansion of lateral shoots relative to main shoots when plants were grown back at cooler temperatures. Not only are young rapidly developing leaves photosynthetically inefficient (Smillie, 1962; Geronimo and Beevers, 1964; Weerakoon et al., 2000), but also the initiation of new shoots and leaves (in this case on the laterals) requires relatively more sucrose per unit dry weight (Xu et al., 1998a). This would have exacerbated the competition for sucrose caused by the unchecked growth of the lateral shoot, leaving less sucrose for translocation to the tubers for conversion into starch.

While the substantial change in leaf area would have a direct impact on plant carbon supply, this may be modulated by the effect of temperature on net photosynthesis per unit leaf area. To date, reports on the effect of elevated temperature on net photosynthesis in potato leaves are inconsistent. Different studies show increased, decreased or no change in photosynthetic rate at the point scale (Hancock et al., 2014; Wolf et al., 1990). Further, there have been no studies on whether effects on photosynthesis persist after the end of a high temperature episode. This is an area that requires further study to understand field responses.

The results of sucrose and starch analysis for the various parts of the plant also support the idea that it was the scarcity of carbon at a whole plant level that depressed tuber dry matter after the high temperature episode. In Expt. 2, there was less sucrose and starch in the tubers at the final sampling and neither sucrose nor starch accumulated in the main shoot leaves or in main stems of the high temperature treatments either at the end of the high temperature period or the final sampling (Figs. 5–8) as might have been expected if the reduction in tuber growth had been a direct primary impact of the treatments (Lafta and Lorenzen, 1995; Basu and Minhas, 1991). At the final sampling of Expt. 1, the data again indicated limiting whole plant carbon supply. The tubers in the

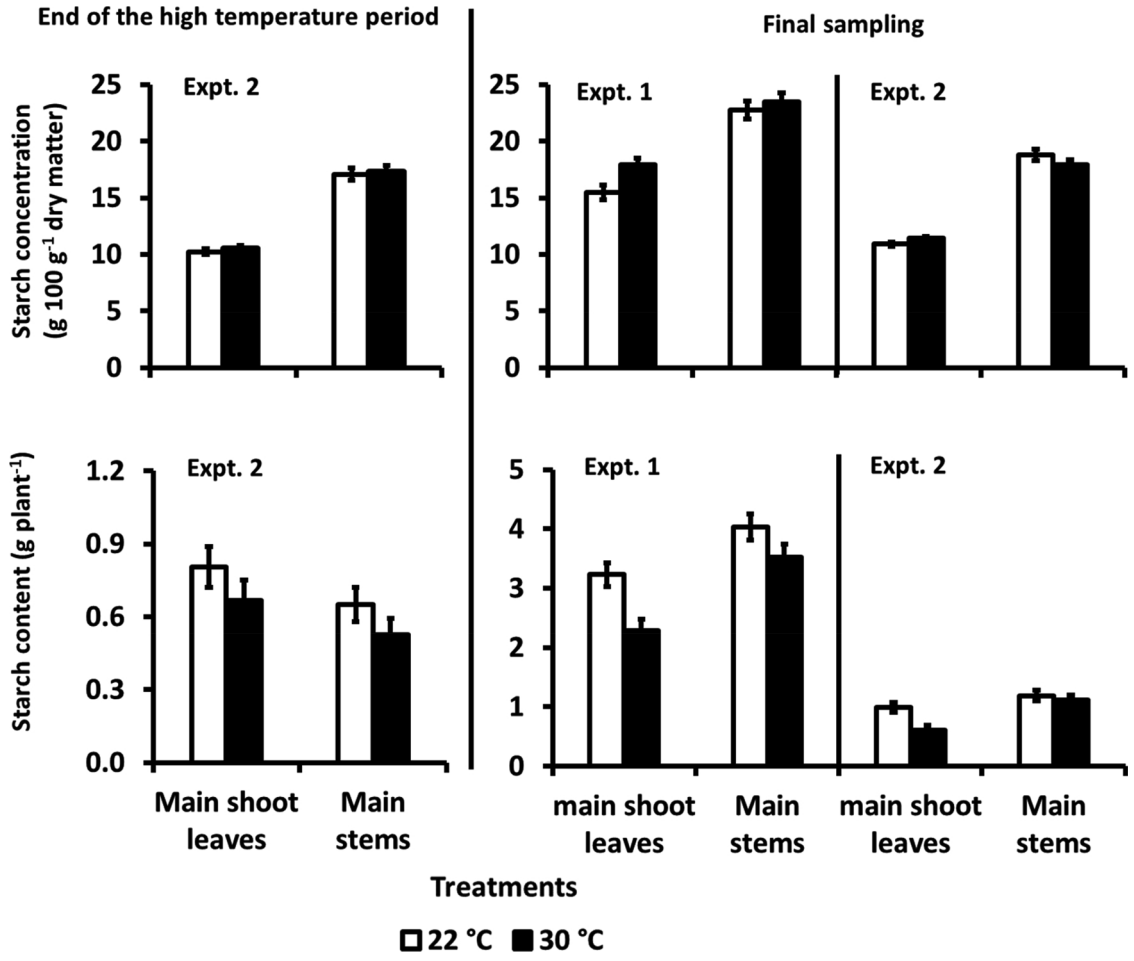


**Fig. 8.** Starch concentration and content in the main shoot leaves and stems at the end of the high temperature period (Expt. 2) and at the final sampling (Expt. 1 and 2) as influenced by a 9-day episode of high temperatures applied before (Expt. 1) or after (Expt. 2) tuber initiation. The high temperatures were applied from 35 to 44 (Expt. 1) and 43 to 52 (Expt. 2) days after planting (DAP), respectively. Error bars are LSD at P = 5%.

high temperature treatments were smaller and had less sucrose and starch content relative to the control. While the main shoot leaves of the high temperature treatments had higher sucrose and starch concentration this was only reflected in higher sucrose content; starch content was lower. Indeed, the increase in sucrose content was an order of magnitude smaller than the reduction in starch content.

The reason for the increase in leaf sucrose concentration and content is unclear. While it might be suggested that the elevated temperatures inhibited sucrose synthase in the leaves during the nine-day episode, and hence conversion of the sucrose to starch, it seems unlikely that the inhibition should persist for 26 days at 22 °C between the end of the episode and the final sampling. It is also inconsistent with the results of Expt. 2. Nösberger and Humphries (1965) observed a feedback mechanism in which a reduction in the growth of the tubers increased the amount of sugar and starch deposits in the stems and leaves. However, no tubers were present at the time that the high temperatures were imposed in Expt. 1, and starch content fell rather than increasing.

It is possible that the tubers in high temperature treatments of Expt. 1 formed fewer cells due to being initiated when the carbon supply was constrained due to reduced leaf area coupled with competition from continued shoot growth (Chen and Setter, 2003, 2012). Tuber cell number is determined relatively early in tuber development (Chen and Setter, 2003, 2012; Xu et al., 1998b) and tubers with fewer cells usually expand less rapidly due to limited starch storage capacity (Xu et al., 1998b; Plaisted, 1957; Reeve et al., 1973). However, again, if this mechanism did cause a feedback to the shoots, increased leaf starch content would have been expected.

The reduction in the tuber dry matter per plant at the final sampling in this study was not likely caused by a reduction in starch synthase activity. Starch synthase is responsible for the incorporation of starch in to potato tubers and hence tuber growth (Mares and Marschner, 1980; Hawker et al., 1979; Geigenberger et al., 1997). However, starch synthase is highly susceptible to high temperatures with activity reducing quickly at temperatures above 25 °C which impairs the conversion of sucrose to starch (Keeling et al., 1993; Jenner, 1994, 1991). The inactivation of starch synthase has been linked to the reduction in tuber growth (Krauss and Marschner, 1984; Krauss, 1981). However, in the current study, tuber yields were not only reduced in plants that had no tubers present during the exposure to high temperatures, there was also less tuber dry matter accumulation after all the plants had been returned to the lower temperature of 22 °C; a temperature that would be optimal for starch synthase activity and hence tuber growth. Further, while the inhibition of starch synthase has been shown to reduce the amount of starch in the tubers, this inhibition also caused the sucrose in the tuber to increase (Mares and Marschner, 1980; Krauss and Marschner, 1984; Geigenberger et al., 1998). In our results, sucrose concentration or content in the tubers was either unchanged or reduced (Figs. 5 and 6).

The results of the current study are not consistent with an increase of gibberellic acid (GA) at high temperatures. Increased GA has been proposed as a mechanism responsible for the reduction in tuber dry matter in potato plants grown at high temperatures (Menzel, 1983). The application of GA on potato plants has been shown to impair tuber initiation and reduce the number of tubers per plant but stimulate the

shoot and stolon growth and stem elongation (Lovell and Booth, 1967; Kumar and Wareing, 1974; Fernie and Willmitzer, 2001). In addition, it is proposed that GA inhibit conversion of sucrose to starch (via inactivation of starch synthase) at the tuber level. Together these effects attributed to GA lead to a reduction in sink size for the deposition of starch and the stimulation of the shoot growth that diverts the dry matter from tubers (Menzel, 1985, 1980, 1983; Gregory, 1956). However, some reports show that tuber dry matter is reduced under high temperatures even when the shoot dry matter is also reduced (Lafta and Lorenzen, 1995).

In our results, there was no indication of tuber initiation being inhibited. Plants in all treatments had the same number or more tubers per plant than the control (Table 1). Further, the length of the main shoot was less at the end of the high temperature period and this continued when plants were grown back at cooler conditions. Rather, after the end of the high temperature period the laterals expanded more than in the controls (Figs. 1–4). Fleisher et al. (2006) also reported that it was the lateral shoots that grew under high temperature, not the main stem. Collectively these responses are more characteristic of an auxin response (Sachs and Thimann, 1967; Kumlay, 2014) than elevated GA.

## 5. Conclusion

a A high temperature episode had both a concurrent and a residual impact on the growth of potato plants and tubers.
b The suppression of tuber growth by the high temperature episode could not be attributed solely to the inactivation of starch synthase because the reduction in tuber growth continued after the end of the high temperature period when plants were again growing at the cooler temperatures (22 °C). Further, in Expt. 1, the reduction in tuber dry matter occurred even though there were no tubers present when the plants were exposed to the high temperature.
c The reduction in tuber yield and the starch content of the tubers was consistent with a reduced carbon supply to the tubers occasioned by reduced plant leaf area concurrent with continued shoot growth.
d Short plants at the end of the high temperature period, together with the stimulation of the lateral shoots after the end of the high temperature period were inconsistent with increased gibberellic acid and more characteristic of an effect of auxins. This requires further exploration.
e Results suggest importance of whole plant carbon dynamics in tuber growth under high temperatures.
f In field conditions, potato plants are exposed to diurnal changes in temperatures, are multi-stemmed and grow in canopy, are predisposed to warmer conditions before hot temperatures events and are exposed to irrigation and nutrition. These differences could alter the importance of the measured responses, and thus warrant further field studies.

## Declarations of interest

None.

## Funding

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

## Authors' contribution

This work was carried out in collaboration of all authors. Author COO designed the study, carried out the actual experiments, collected the data, conducted statistical analysis and wrote the first draft under the supervision of authors SM and RB. The final draft was read and approved by all authors.

## Acknowledgements

COO thanks the Australia Government for financial support through a Research Training Program Scholarship. Thanks to the State Agricultural Biotechnology Centre and the Centre for Biosecurity and Food Security, Murdoch University for use of facilities and to Bob Du (Centre for Biosecurity and Food Security) for assistance with sucrose and starch analysis.

## References

Albalasmeh, A.A., Berhe, A.A., Ghezzehei, T.A., 2013. A new method for rapid determination of carbohydrate and total carbon concentrations using UV spectrophotometry. Carbohydr. Polym. 97 (2), 253–261.
Basu, P.S., Minhas, J.S., 1991. Heat tolerance and assimilate transport in different potato genotypes. J. Exp. Bot. 42 (240), 861–866.
Booth, A., Lovell, P.H., 1972. The effect of pre-treatment with gibberellic acid on the distribution of photosynthate in intact and disbudded plants of *Solanum tuberosum* L. New Phytol. 71 (5), 795–804.
Borah, M.N., Burt, R.L., Headford, D.W.R., Milthorpe, F.L., Sadler, E.M., 1960. Growth of the potato plant. Ann. Appl. Biol. 48 (2), 433–434.
Boyd, N.S., Gordon, R., Martin, R.C., 2002. Relationship between leaf area index and ground cover in potato under different management conditions. Potato Res. 45 (2), 117–129.
Bushnell, J., 1927. The relation of temperature to growth and respiration in the potato plant. Am. Potato J. 4 (9), 119.
Chen, C.-T., Setter, T.L., 2003. Response of potato tuber cell division and growth to shade and elevated $CO_2$. Ann. Bot. 91 (3), 373–381.
Chen, C.-T., Setter, T.L., 2012. Response of potato dry matter assimilation and partitioning to elevated $CO_2$ at various stages of tuber initiation and growth. Environ. Exp. Bot. 80, 27–34.
Driver, C.M., Hawkes, J.G., 1943. Photoperiodism in the potato. Imp. Bur. Plant Breed. Genet. Cambridge.
Duarte-Delgado, D., Narváez-Cuenca, C.-E., Restrepo-Sánchez, L.-P., Kushalappa, A., Mosquera-Vásquez, T., 2015. Development and validation of a liquid chromatographic method to quantify sucrose, glucose, and fructose in tubers of *Solanum tuberosum* L. Group Phureja. J. Chromatogr. B 975, 18–23.
Dubois, M., Gilles, K.A., Hamilton, J.K., Rebers, P., Smith, F., 1956. Colorimetric method for determination of sugars and related substances. Anal. Chem. 28 (3), 350–356.
Edwards, A., Fulton, D.C., Hylton, C.M., Jobling, S.A., Gidley, M., Rössner, U., Martin, C., Smith, A.M., 1999. A combined reduction in activity of starch synthases II and III of potato has novel effects on the starch of tubers. Plant J. 17 (3), 251–261.
Fernie, A.R., Willmitzer, L., 2001. Molecular and biochemical triggers of potato tuber development. Plant Physiol. 127 (4), 1459–1465.
Fleisher, D.H., Timlin, D.J., Reddy, V.R., 2006. Temperature influence on potato leaf and branch distribution and on canopy photosynthetic rate. Agron. J. 98 (6), 1442–1452.
Geigenberger, P., Reimholz, R., Geiger, M., Merlo, L., Canale, V., Stitt, M., 1997. Regulation of sucrose and starch metabolism in potato tubers in response to short-term water deficit. Planta 201 (4), 502–518.
Geigenberger, P., Geiger, M., Stitt, M., 1998. High-temperature perturbation of starch synthesis is attributable to inhibition of ADP-glucose pyrophosphorylase by decreased levels of glycerate-3-phosphate in growing potato tubers. Plant Physiol. 117 (4), 1307–1316.
Geronimo, J., Beevers, H., 1964. Effects of aging and temperature on respiratory metabolism of green leaves. Plant Physiol. 39 (5), 786.
Gregory, L.E., 1956. Some factors for tuberization in the potato plant. Am. J. Bot. 43 (4), 281–288.
Haebel, S., Hejazi, M., Frohberg, C., Heydenreich, M., Ritte, G., 2008. Mass spectrometric quantification of the relative amounts of C6 and C3 position phosphorylated glucosyl residues in starch. Anal. Biochem. 379 (1), 73–79.
Hancock, R.D., Morris, W.L., Ducreux, L.J.M., Morris, J.A., Usman, M., Verrall, S.R., Fuller, J., Simpson, C.G., Zhang, R., Hedley, P.E., Taylor, M.A., 2014. Physiological, biochemical and molecular responses of the potato (*Solanum tuberosum* L.) plant to moderately elevated temperature. Plant Cell Environ. 37 (2), 439–450.
Haverkort, A.J., 1990. Ecology of potato cropping systems in relation to latitude and altitude. Agric. Syst. 32 (3), 251–272.
Hawker, J.S., Marschner, H., Krauss, A., 1979. Starch synthesis in developing potato tubers. Physiol. Plant. 46 (1), 25–30.
Hawkes, J.G., 1978. History of the potato. In: Harris, P.M. (Ed.), The Potato Crop. Springer, Dordrecht, pp. 1–12.
Hijmans, R.J., 2003. The effect of climate change on global potato production. Am. J. Potato Res. 80 (4), 271–279.
Hou, X., Wang, F., Han, J., Kang, S., Feng, S., 2010. Duration of plastic mulch for potato growth under drip irrigation in an arid region of Northwest China. Agric. For. Met. 150 (1), 115–121.
Ingram, K.T., McCloud, D.E., 1984. Simulation of potato crop growth and development. Crop Sci. 24 (1), 21–27.
Jenner, C., 1991. Effects of exposure of wheat ears to high temperature on dry matter accumulation and carbohydrate metabolism in the grain of two cultivars. I. Immediate responses. Funct. Plant Biol. 18 (2), 165–177.
Jenner, C., 1994. Starch synthesis in the kernel of wheat under high temperature conditions. Funct. Plant Biol. 21 (6), 791–806.

Jovanovic, Z., Stikic, R., Brocic, Z., Oljaca, J., 2012. Climate change: challenge for potato production in South-East Europe. In: Caprara, C. (Ed.), Potatoes: Production, Consumption and Health Benefits. Nova Science, New York, USA, pp. 37–66.
Keeling, P., Bacon, P., Holt, D., 1993. Elevated temperature reduces starch deposition in wheat endosperm by reducing the activity of soluble starch synthase. Planta 191 (3), 342–348.
Kim, Y.-U., Seo, B.-S., Choi, D.-H., Ban, H.-Y., Lee, B.-W., 2017. Impact of high temperatures on the marketable tuber yield and related traits of potato. Eur. J. Agron. 89, 46–52.
Kooman, P.L., 1995. Yielding ability of potato crops as influenced by temperature and daylength. Research Institute for Agrobiology and Soil Fertility Theoretical Production Ecology. pp. 155 Wageningen.
Krauss, A., 1981. Effect of high tuber temperature on tuber growth and starch accumulation. Proceedings of the International Symposium on 'Potatoes in Hot Climates'.
Krauss, A., Marschner, H., 1984. Growth rate and carbohydrate metabolism of potato tubers exposed to high temperatures. Potato Res. 27 (3), 297–303.
Kumar, D., Wareing, P.F., 1974. Studies on tuberization of *Solanum andigena*. New Phytol. 73 (5), 833–840.
Kumlay, A.M., 2014. Combination of the Auxins NAA, IBA, and IAA with $GA_3$ improves the commercial seed-tuber production of potato (*Solanum tuberosum* L.) under in vitro conditions. BioMed Res. Int. 1–7.
Lafta, A.M., Lorenzen, J.H., 1995. Effect of high temperature on plant growth and carbohydrate metabolism in potato. Plant Physiol. 109 (2), 637–643.
Lovell, P.H., Booth, A., 1967. Effects of gibberellic acid on growth, tuber formation and carbohydrate distribution in potato (*Solanum tuberosum* L.). New Phytol. 66 (4), 525–537.
Mares, D.J., Marschner, H., 1980. Assimilate conversion in potato tubers in relation to starch deposition and cell growth. Ber. Bot. Ges. 93 (1), 299–313.
Mares, D.J., Marschner, H., Krauss, A., 1981. Effect of gibberellic acid on growth and carbohydrate metabolism of developing tubers of potato (*Solanum tuberosum* L.). Physiol. Plant. 52 (2), 267–274.
Marinus, J., Bodlaender, K., 1975. Response of some potato varieties to temperature. Potato Res. 18 (2), 189–204.
Menzel, C.M., 1980. Tuberization in potato at high temperatures: responses to gibberellin and growth inhibitors. Ann. Bot. 46 (3), 259–265.
Menzel, C.M., 1983. Tuberization in potato at high temperatures: gibberellin content and transport from buds. Ann. Bot. 52 (5), 697–702.
Menzel, C.M., 1985. Tuberization in potato at high temperatures: interaction between temperature and irradiance. Ann. Bot. 55 (1), 35–39.
Monteith, J.L., Moss, C., 1977. Climate and the efficiency of crop production in Britain. Philos. Trans. R. Soc. Lond. B 281 (980), 277–294.
Moorby, J., 1978. The physiology of growth and tuber yield. In: Harris, P.M. (Ed.), The Potato Crop. Springer, Boston, USA, pp. 153–194.
Morita, S., Yonemaru, J.-I., Takanashi, J.-I., 2005. Grain growth and endosperm cell size under high night temperatures in rice (*Oryza sativa* L.). Ann. Bot. 95 (4), 695–701.
Muthoni, J., Kabira, J., 2015. Potato production in the hot tropical areas of Africa: progress made in breeding for heat tolerance. J. Agric. Sci. 7 (9), 220–227.
Nösberger, J., Humphries, E.C., 1965. The influence of removing tubers on dry-matter production and net assimilation rate of potato plants. Ann. Bot. 29 (4), 579–588.
Pereira, A.B., Augusto, N., Ramos, V.J., Pereira, A.R., 2008. Potato potential yield based on climatic elements and cultivar characteristics. Bragantia 67 (2), 327–334.
Plaisted, P.H., 1957. Growth of the potato tuber. Plant Physiol. 32 (5), 445–453.
Prange, R.K., McRae, K.B., Midmore, D.J., Deng, R., 1990. Reduction in potato growth at high temperature: role of photosynthesis and dark respiration. Am. Potato J. 67 (6), 357–369.
Prasad, P., Pisipati, S., Ristic, Z., Bukovnik, U., Fritz, A., 2008. Impact of nighttime temperature on physiology and growth of spring wheat. Crop Sci. 48 (6), 2372–2380.
Reeve, R.M., Timm, H., Weaver, M.L., 1973. Parenchyma cell growth in potato tubers II. Cell divisions vs cell enlargement. Am. Potato J. 50 (3), 71–78.
Reynolds, M.P., Ewing, E.E., 1989. Effects of high air and soil temperature stress on growth and tuberization in *Solanum tuberosum* L. Ann. Bot. 64 (3), 241–247.
Rykaczewska, K., 2015. The effect of high temperature occurring in subsequent stages of plant development on potato yield and tuber physiological defects. Am. J. Potato Res. 92 (3), 339–349.
Sachs, T., Thimann, K.V., 1967. The role of auxins and cytokinins in the release of buds from dominance. Am. J. Bot. 54 (1), 136–144.
Savin, R., Nicolas, M.E., 1996. Effects of short periods of drought and high temperature on grain growth and starch accumulation of two malting barley cultivars. Funct. Plant Biol. 23 (2), 201–210.
Smillie, R.M., 1962. Photosynthetic and respiratory activities of growing pea leaves. Plant Physiol. 37 (6), 716–721.
Struik, P.C., Geertsema, J., Custers, C.H., 1989a. Effects of shoot, root and stolon temperature on the development of the potato (*Solanum tuberosum* L.) plant. III. Development of tubers. Potato Res. 32 (2), 151–158.
Struik, P.C., Geertsema, J., Custers, C.H., 1989b. Effects of shoot, root and stolon temperature on the development of the potato (*Solanum tuberosum* L.) plant. I. Development of the haulm. Potato Res. 32 (2), 133–141.
Timlin, D., Rahman, S.M.L., Baker, J., Reddy, V.R., Fleisher, D., Quebedeaux, B., 2006. Whole plant photosynthesis, development, and carbon partitioning in potato as a function of temperature. Agron. J. 98 (5), 1195–1203.
Van Dam, J., Kooman, P.L., Struik, P.C., 1996. Effects of temperature and photoperiod on early growth and final number of tubers in potato (*Solanum tuberosum* L.). Potato Res. 39 (1), 51–62.
Weerakoon, W.M.W., Ingram, K.T., Moss, D.N., 2000. Atmospheric carbon dioxide and fertilizer nitrogen effects on radiation interception by rice. Plant Soil 220 (1–2), 99–106.
Wheeler, R., Steffen, K., Tibbitts, T., Palta, J., 1986. Utilization of potatoes for life support systems II. The effects of temperature under 24-H and 12-H photoperiods. Am. Potato J. 63 (11), 639–647.
Wolf, S., Olesinski, A.A., Rudich, J., Marani, A., 1990. Effect of high temperature on photosynthesis in potatoes. Ann. Bot. 65 (2), 179–185.
Xu, X., van Lammeren, A., Vermeer, E., Vreugdenhil, D., 1998a. The role of gibberellin, abscisic acid, and sucrose in the regulation of potato tuber formation in vitro. Plant Physiol. 117 (2), 575–584.
Xu, X., Vreugdenhil, D., van Lammeren, A., 1998b. Cell division and cell enlargement during potato tuber formation. J. Exp. Bot. 49 (320), 573–582.